

Biology of *Polyrhachis schellerichae*, a specialized bamboo-dwelling ant species from the Malay Peninsula (Insecta: Hymenoptera: Formicidae)

ANGELA L. SCHELLERICH-KAADEN, WOLFGANG H. O. DOROW, CAROLINE LIEFKE,
RÜDIGER W. KLEIN & ULRICH MASCHWITZ

With 2 figures and 5 tables

Abstract

The biology of the recently discovered bamboo-dwelling ant species *Polyrhachis schellerichae* DOROW 1996, a member of the *P. (Myrmhopla) hector*-species group, was investigated in Selangor, West-Malaysia. It was found nesting in culm internodes of giant bamboo (Bambusoidea: *Gigantochloa thooii*). The investigated colonies were polydomous, diurnal and lived in tight trophobiosis with a pseudococcid, *Kermicus wroughtoni* NEWSTEAD 1897, which were kept inside the nest internodes. The trophobiotic partners were transported to new nest internodes during colony enlargement or nest moves. A series of specific morphological and biological features indicate that this ant is specialized on living within giant bamboo culms. *P. schellerichae* is compared with the other ant species also specialized on giant bamboo. For the plants no advantage could be observed so far. This association is seen as a case of mild parasitism.

Key words: Formicidae, *Polyrhachis schellerichae*, Bambusoidea, *Gigantochloa thooii*, South East Asia, Malaysia, Pseudococcidae, *Kermicus wroughtoni*.

Introduction

Myrmecophytism is an important and well known phenomenon in Old and New World tropical rain forests (BEATTIE 1985, HUXLEY & CUTLER 1991, JOLIVET 1986, DAVIDSON & McKEY 1993). In myrmecophytic associations ants and plants live together in a mutualistic way. While the ants protect their plant partners against herbivores and plant competitors or provide them with nutrients, the plants offer their ant partners domatia, i.e., special structures for nesting and additionally often provide them with food.

DOROW & MASCHWITZ (1990) recently described from South East Asia the hitherto unknown phenomenon of a one-sided host-plant-specialization in ants, without the interactive benefits characteristic for myrmecophytic relationships. Here the ant species are tightly adapted to their host plants. The plants, species of large tropical bamboo, however, do not actively provide the ants with nesting space. No advantage for the plant could be detected so far. Up to now we know three ant species showing this non-

mutualistic specialization on nesting in and on bamboo: *Polyrhachis arachne* EMERY 1896, *P. hodgsoni* FOREL 1902 (DOROW & MASCHWITZ 1990) and *Tetraponera* sp. near *attenuata* F. SMITH 1877 (KLEIN et al. 1992, BUSCHINGER et al. 1994).

With 470 described species the well known palaeotropical genus *Polyrhachis* SMITH 1857 is one of the largest ant genera of the world (DOROW 1995, DOROW & KOHOUT 1995). A large species of this genus, described by DOROW (1996), was discovered during our field research on bamboo-dwelling ants in West Malaysia. The new species belongs to the *hector*-group of the subgenus *Myrmhopla*. Compared with the other members of this group, *Polyrhachis schellerichae* shows remarkable morphological and biological differences. Its biology shows great similarities to that of the above-quoted bamboo specialists. Here we present results which indicate that *P. schellerichae* is very likely another bamboo specialist.

Authors' addresses:

A. L. SCHELLERICH-KAADEN, C. LIEFKE, R. W. KLEIN & U. MASCHWITZ, Zoologisches Institut der Universität, Siesmayerstraße 70, D-60054 Frankfurt am Main. — W. H. O. DOROW, Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325 Frankfurt am Main.

Material and methods

All observations were carried out around the Ulu Gombak Field Studies Centre of the University Malaya (30 km northeast of Kuala Lumpur, 240–500 m a. s. l.). Although timber extraction has created a secondary lowland forest with areas where bamboos have become dominant (BISHOP 1973) there are remnants of hill dipterocarp forest (FIALA 1988). Bamboo identification was accomplished using the taxonomic works of HOLTUM (1958), WIDJAJA (1987), DRANSFIELD (1992) and WONG (1992).

The culms of two bamboo-groves inhabited by two *P. schellerichae* colonies were cut down and searched thoroughly for ants. Biological data such as nest-type, nest height, presence or absence of trophobionts, etc., were collected. After the opening of the nest-internode the ants were killed with ethylacetate and afterwards transferred to 70% alcohol for identification and counting. The colony size was calculated taking the number of collected workers plus an estimated number of workers that in some cases escaped during the process of opening the nest-internode. Five of the partial nests of colony 1 that could not be sampled contributed to the colony size the mean number of workers, males and alate queens of the counted nests.

The second colony was found nesting in the culm internodes of two bamboo clumps about 2 m apart from each other with 16 and 19 culms respectively. Only one clump was felled and the partial nests¹⁾ in this clump were sampled for colony size calculation. The groves of colony 1 and 2 were about 50 m apart and separated from each other.

Food recruitment tests were carried out in the field. These experiments consisted of two parts. During the con-

trol part for half an hour every minute all ants leaving the nest were counted. In this time no food was presented. The second part started with the offering of food (honey solution, insect pieces or human urine). Then every minute all ants leaving the nest were counted until their number decreased again to the initial level. We compared the total number of ants leaving the nest during the control part with the total number of those leaving the nest during the first 30 min of the food donation part. In addition we made recruitment tests in our laboratory (in Frankfurt). Here honey water was offered as food. Before each test the ants were kept for three to six days without food. In contrast to the field tests the ants had to cross a Y-shaped bridge system to reach the food which was presented on one side of the bridge. Here we compared the total number of ants crossing either the food side or the control side of the bridge. The two parts of the tests were evaluated separately. The data of the field experiments were tested with the Chi-Square-Test, those of the laboratory experiments with the Sign-Test (SIEGEL 1987).

Nest relocation experiments were carried out in the laboratory of the field station. The original nest internode was opened and a new internode with an artificial circular hole in its wall was offered. After the nest relocations we opened the new internodes to check for the transport of trophobionts into the new nest.

During March and July to September 1993 five day (7.45–18.30 h) and two night (18.30–7.30 h) activity counts were conducted in the field. They consisted of registering the numbers of workers leaving or entering the nest entrances of two partial nests for a 10 minute period each hour.

Results

Colony structure and colony size

Two colonies of *P. schellerichae* were found nesting in culm internodes of a large tropical bamboo, most probably *Gigantochloa thooii* WONG 1992.²⁾ Both colonies were polydomous. Colony 1 could be censused almost completely. Colony 2 was collected only in part. Partial nests of *P. schellerichae* were found in 24 and 7 culms of the respective groves (Table 1). The two colonies were found to use 47 and 16 culm internodes respectively, representing 37% and 30% of the accessible internodes (Table 1), and 1 to 6 (median = 2; $n = 31$) internodes per inhabited culm. Other ant species (Table 1 and 2) inhabited 28% and 33% of the available culm internodes. The accessible culm internodes were to a minor degree (3% and 11%) also used by other animals such as other insects, spiders, bats or snakes (Table 1). 32% and 26% of the accessible culm internodes of each grove were not colonized at all.

Both colonies contained several thousand workers and alates constituted 27% and 31% of total adults (Table 3).

Brood and trophobionts (see below) were present in every partial nest with the exception of one broodless nest in each colony with only several (3 and 20) workers and a few mealybugs. Supposedly these were internodes only very recently entered during colony expansion. In colony 1 three dealate queens were found in partial nests of different culms, but two of them were already dead when sampled and nearly all their extremities had been severed from the body. So only one queen was found in normal condition. No dealate queen was found in the censused part of colony 2. These findings suggest that the species is monogynous.

Nest structure

P. schellerichae nests inside the culm internodes (mean length 42.66 ± 11.49 cm, $n = 42$; mean diameter 8.11 ± 1.65 cm, $n = 40$). The interior of all investigated nest internodes ($n = 63$) was neither covered with silk nor modified in any other way. Larval silk was only used to attach the

¹⁾ Partial nest = one of the nests of a polydomous colony.

²⁾ This species is often misidentified with *G. levis*. According to WONG (1992) *G. levis* is confined to East Malaysia and the species found in West Malaysia is *G. thooii*.

Table 1. Utilization of accessible culm internodes by ants and other animals.

	Colony 1	%	Colony 2*	%
Culms present in the grove	36	100	19	100
Culms with accessible internodes	33	91.67	15	78.95
Culms inhabited by <i>Polyrhachis schellerichae</i>	24	66.67	7	36.84
Accessible culm internodes in the grove	128	100	54	100
Number of accessible culm internodes per culm (median)	3.42	—	3.25	—
Accessible culm internodes inhabited by <i>Polyrhachis schellerichae</i>	47	36.72	16	29.63
Accessible culm internodes inhabited by other ants	36	28.13	18	33.33
Accessible culm internodes inhabited by other animals	4	3.12	6	11.11
Vacant accessible culm internodes	41	32.03	14	25.93

* Only one clump of this grove was felled, see „Material and methods“, so this colony was not sampled in toto.

Table 2. List of other ant species using culm internodes as nesting or feeding sites in the *P. schellerichae* inhabited groves.

Colony 1		Colony 2	
Ant species	Number of used culm internodes	Ant species	Number of used culm internodes
<i>Tetraponera</i> sp. 1	2	<i>Cataulacus</i> sp. 2	2
<i>Cataulacus</i> sp. 1	7	<i>Crematogaster</i> sp. 1	2
<i>Crematogaster</i> sp. 4	14	<i>Crematogaster</i> sp. 6	8
<i>Crematogaster</i> sp. 5	1	<i>Crematogaster</i> sp. 7	1
<i>Crematogaster</i> sp.	5	<i>Polyrhachis arachne</i>	5
<i>Camponotus</i> sp. 1	4		
<i>Camponotus</i> sp. 3	2*		
<i>Polyrhachis arachne</i>	2		

* Sharing these two internodes with *Crematogaster* sp. 4.

brood to the internode walls. In case of disturbance the workers detached the threads and carried the brood away. The pupae of *P. schellerichae* have cocoons. An occupied culm internode had usually one oval nest entrance (length 2.0–15.0 mm; width 1.0–6.0 mm; n = 11). Only exceptionally more than one nest entrance (up to three) per nest internode could be observed. The nest entrances of *P. schellerichae* were always guarded by one to several workers depending on the size of the hole. During rain the number of guarding workers at the nest entrances increased. Their heads blocked the nest entrance from inside and thus apparently prevented influx of rain water into the nest. The head of *P. schellerichae*, especially that of the queen, is remarkably elongated.

During one of our nest relocation experiments we could observe that workers of *P. schellerichae* were trying to enlarge a nest entrance.

Nest hygiene

During the field studies we observed two workers that were throwing particles out of the nest entrance. As we cut off one partial nest and placed it in a plastic basin at the field station we witnessed six workers throwing particles of debris and one dead larva out of the nest entrance. After a while a small pile accumulated on the ground below the nest entrance. The same phenomenon could be observed

Table 3. Colony size of *Polyrbachis schellerichae*. The number of workers was calculated as described under "Material and methods".

	Colony 1	Colony 2*
Workers	7203	2693
Number of workers per partial nest (median)	123**	153.5***
Dealate queens	1	—
Alate queens	605	229
Alate males	1310	594

* Not collected in toto.

** n = 38; range = 7–432 workers;

*** n = 16; range = 21–297 workers.

when we transferred two partial nests to our laboratory in Germany. Although we did find small debris particles on the bottoms of the nest internodes these never amounted to the quantities found in nest internodes of *Polyrbachis arachne* where up to 10 cm of the internode bottom were covered with debris. The nest internodes of *P. arachne* contained an average of 687 workers (median) (n = 10, range: 125–1088 workers) (SCHELLERICH, unpublished observations) which is about four to five times more workers than found in *P. schellerichae* nest internodes (Table 3).

Although the influx of rain water was prevented in the above described manner, small amounts of water were sometimes found inside the partial nests of *P. schellerichae*. From one of the bamboo specialists, *Tetraponera* sp. near *attenuata*, a special water removal behaviour is known (KLEIN et al. 1993). To check whether *P. schellerichae* is also able to bail water from its nest internodes we conducted two tests in the field and three in our laboratory. In the field and in the laboratory we injected coloured water with a syringe into two naturally inhabited internodes and three artificial nests. We observed the nest entrances for two hours after each injection and again after 24 hours. In both cases no water bailing behaviour could be provoked.

Nutrition and recruitment behaviour

P. schellerichae lives in tight trophobiosis with *Kermicus wroughtoni* NEWSTEAD 1897 (Pseudococcidae). Numerous trophobionts were present in all partial nests of *P. schellerichae*. They were sitting all over the internode walls and often concentrated on the upper part of the internode and on the nodus septum that separates the internodes. One nest internode checked for the number of trophobionts contained 188 crawlers and 10 adult trophobionts.

No hunting activity or retrieval of recognizable prey items could be observed during the activity counts. Several workers however were observed carrying faeces (presumably from birds or reptiles) from the ground into the nest. Only two of five recruitment tests in the field resulted in a significant recruitment behaviour (Table 4). The offer of human urine resulted both times in recruitment activities of *P. schellerichae*, one of the tests was significant (Table 4). Offered insect pieces once triggered a significant recruit-

Table 4. Recruitment behaviour of *Polyrbachis schellerichae* in the field, evaluated with the Chi-Square-Test. Number of ants leaving the nest counted half an hour before food donation and counted after food donation until their number decreased to the initial level.

Food	Control part	After food donation	X ²	p
Insect pieces	7	7	0	1
Insect pieces	4	14	4.50	0.05*
Honey water	4	9	1.23	0.15
Mammal urine	5	13	2.72	0.1
Mammal urine	5	16	4.76	0.05*

X² = Chi-Square-value, p = probability, * = significant test.

ment behaviour (Table 4). The second offer of insect pieces was mostly ignored which was due to heavy competition at the bait from *Polyrbachis arachne*. Honey solution offered to the workers outside the nest was ignored in two of three cases. We suppose that the honeydew excreted from the trophobionts inside the nest constitutes the main source of nutrition for *P. schellerichae*. Additionally small amounts of dead insects and faeces add to the diet. Very often we could see workers with dilated gasters transporting food in a liquid form between the nests, very likely honeydew from the trophobionts inside the nests.

Table 5. Recruitment behaviour of *Polyrbachis schellerichae* in the laboratory, evaluated with the sign-test. Number of ants leaving the nest counted half an hour before food donation and counted after food donation until their number decreased to the initial level.

Starvation days	Control part			After food donation		
	f>c	f<c	p	f>c	f<c	p
3	3	3	*	26	0	0,001
3	8	5	0,855	25	0	0,001
3	5	6	0,969	27	0	0,001
4	8	8	1	29	0	0,001
4	7	5	0,938	24	0	0,001
6	3	3	*	27	0	0,001
6	2	1	*	26	0	0,001
6	2	1	*	28	0	0,001

* Matched pairs <5, below test-niveau;

f>c matched pairs food bridge/control bridge, food bridge > control bridge;

f<c matched pairs food bridge/control bridge, food bridge < control bridge;

p probability.



Fig. 1. Nest movement of *Polyrbachis schellerichae*. — a) Males are carried by the neck; b) queens walk by themselves, and c) trophobionts are taken between the mandibles and carried to the new nest.

In all tests the recruited ants found their way to the bait independently without any leading animal. Some *P. schellerichae* workers showed a characteristic behaviour when heading back to the nest or again from the nest to the food source. They moved forward at a slow pace and pressed their gaster tip to the ground at frequent intervals. This behaviour is known from other ant species when laying odour trails (HÖLLDOBLER & WILSON 1990).

All laboratory tests showed a significant number of ants (Sign-Test, $p = 0.001$) on the food side of the bridge system after food offering (Table 5). We found an increase in the total number of ants on the food bridge from 3 to 10 (mean = 5.8 workers) in the control part of the test to 58 to 158 (mean = 101.2 workers) in the food donation part. The total number of ants on the control bridge was in both parts of the tests on the same level, 2 to 10 ants (mean number = 5.0) in the control part and 1 to 9 ants (mean number = 4.8) after food donation.

Nest relocation and mealybug transport

If a suitable new internode was located by scouts of an opened nest the relocation was completed in relatively short time (1.5 and 3 h, $n = 2$). Whereas males were carried, alate queens and workers walked independently to the new nest. The males were seized in the neck and carried in front of the worker (Fig. 1a). Only once a worker was carried. It was held by the mandibles in the typical formicine way with its body under the head of the carrying worker. The nest relocations followed no fixed time pattern. Males and brood were carried during the whole time. The alate queens walked either by themselves amidst a group of workers or individually without accompanying workers (Fig. 1b). Workers carrying trophobionts (Fig. 1c) to the new nest-site were observed in five cases during two nest relocations. Only crawlers (1st instar larvae) were carried and only a fraction of the crawlers of the original nest was transferred to the new nest-site. All new nest internodes contained living trophobionts when they were open-

ed a few days later ($n = 4$). As these crawlers sat on the internode walls in the same way as the others left behind in the old nest internode we concluded that they were not taken as prey but as trophobiotic partners instead. Under natural conditions in the field we also observed this pseudococcid carried by *P. schellerichae* between partial nests in two cases. These transports were not connected with nest relocation.

Activity outside the nest and territorial behaviour

Our studies on the activity of *P. schellerichae* outside the nest revealed the species to be strictly diurnal. Workers were detected outside the nest from 8.00 h until 19.00 h local time (Fig. 2). During rain activity generally dropped to zero. Only once during our activity counts two workers left the nest during rain. Another time four workers left the nest shortly after raining had stopped and water was still dropping from the vegetation.

The workers of *P. schellerichae* forage individually as a rule. Most of the workers leaving a nest did not forage but hurried without any delay to other nest internodes. Traffic between the partial nests was accomplished via distinct routes up and down the culm. Neighbouring culms were connected through routes on the ground and presumably through routes in the canopy of the culms over branches and leaves which often are in very close contact. Transport of brood and mealybugs to partial nests was also observed.

A small fraction of the workers leaving the nest followed the routes on the ground only for a short distance, then left the route in any direction, often walking in small loops, i.e., displaying searching behaviour. These workers were also observed to forage on other plants in the vicinity of the nest culm. We assume that the workers that retrieved animal faeces belonged to this small group of foraging ants.

Many times single workers emerged from the nest entrance and more or less directly returned into the nest. Often such workers walked at least one time around the

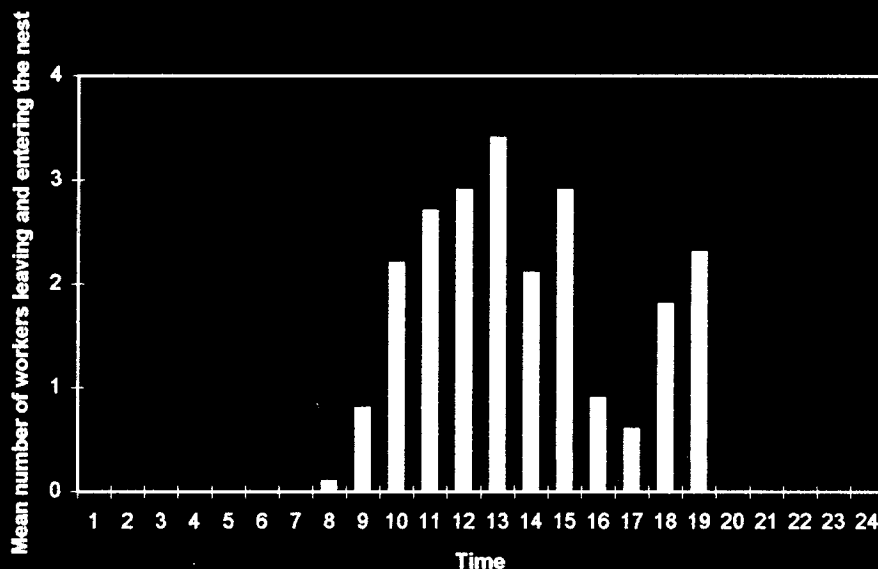


Fig. 2. Activity pattern of *Polyrhachis schellerichae*. Summary of five day (7.45–18.30 h) and two night (18.30–7.30 h) activity counts in the field carried out in March, July and September 1993. The mean number of workers leaving and entering the nest during 10 minutes of observation per hour is given, the results of all activity counts are summarized.

nest entrance before disappearing inside the nest again. Others just sat next to the nest entrance for a short time. Sometimes a worker moved in loops around the nest entrance. During the five day activity counts altogether 24 workers (all from the same partial nest) were observed displaying such a behaviour, 19 of these workers returned into the nest and 5 walked at least up or down the culm and even on the ground before returning into the nest. We presume that these workers are either guards of the nest entrance or young workers that have hitherto performed activities inside the nest and now become acquainted with activities outside the nest. Other species of *Polyrhachis*, e.g., *P. arachne*, *P. muelleri*, *P. illaudata*, show a comparable patrolling behaviour at their nest entrances.

Although *P. schellerichae* was observed to maintain a route over a branch lying on the ground for at least 7

months (March to September 1993), it showed no territorial behaviour when encountering other ants of the genus *Polyrhachis* or an unidentified ponerine ant on that route ($n = 2$) but behaved in an evasive way, as did the encountered species. Once a single small myrmicine was observed to chase *P. schellerichae* from that branch. When a bait was offered ($n = 5$), *P. schellerichae* was dominated by *P. arachne*. *P. arachne* workers attacked *P. schellerichae* workers by biting their legs or other parts of their body and *P. schellerichae* then often retreated from the bait. Two times a fight between workers of the two species ended with both workers falling to the ground. We also observed a *Crematogaster* species at the bait ($n = 2$) which dominated both *Polyrhachis* species. *Polyrhachis hector* once visited the bait but did not engage in struggles with the other *Polyrhachis* species.

Discussion

Bamboo species, mainly giant forms, are very common plants in the tropical regions of South East Asia. Especially their hollow culm internodes, which often are opened by wood-boring insects, birds or mammals, offer a widespread and well accepted microhabitat for many animals (MEDWAY & MARSHALL 1970, 1972, CORBET 1983, KURIHARA 1983, KOVAC 1994, WINKLER et al. 1995, SCHELLERICH & MASCHWITZ, unpublished observations). Additionally the branch internodes and the branch and leaf insertions offer well suited shelters for many small arboreal ants (SCHELLERICH & MASCHWITZ, in preparation). So these tropical giant bamboos are of unique and eminent ecological significance

in their habitats as they are a fast growing, common and constant source of microhabitats for all kinds of animals, especially ants.

During our investigations on bamboo inhabiting ants and their trophobionts (MASCHWITZ et al. 1986, 1987, 1988, DOROW & MASCHWITZ 1990, KLEIN et al. 1992, 1993, BUSCHINGER et al. 1994) we recently discovered that some ant species are highly specialized on bamboo in a one-sided way (DOROW & MASCHWITZ 1990, KLEIN et al. 1992, BUSCHINGER et al. 1994). On the plant side no mutualistic coadaptations such as the provisioning of specialized nesting space (domatia) could be recognized. Some bamboo

species however, possess extrafloral nectaries, especially on their young shoots (MASCHWITZ et al. 1986, KOVAC 1994, SCHELLERICH & MASCHWITZ, in preparation). Extrafloral nectaries are common in many other tropical rainforest plants (BENTLEY & ELIAS 1983, OLIVEIRA & OLIVEIRA-FILHO 1991, FIALA et al. 1994) and there is growing evidence that ants visiting these structures protect the plants against herbivores (BENTLEY 1977, BUCKLEY 1982, JOLIVET 1986, KOPTUR 1992).

Many details of the morphology and sociobiology of *P. schellerichae* indicate that this ant is specialized to nest in the hollow culm internodes of giant bamboos.

Morphology

P. schellerichae belongs to the *Polyrbachis* (*Myrmhopla*) *hector* species group. This group is distinguished from all other *Polyrbachis* species by flattened tibiae and scapes. The species are large and slender with long legs giving these ants a spider-like appearance. In comparison to other members of the species group in *P. schellerichae* the head of the worker and especially that of the queen is extremely elongated. Only one further member of the *hector*-group, a hitherto undescribed species (DOROW, in preparation) is relatively similar to *P. schellerichae* in this respect but, nothing is known about its biology.

As we have no direct observations concerning colony foundation and nest entrance blocking by queens we can only speculate about the meaning of the extraordinary morphology of *P. schellerichae*. Most of the entrance holes in culm internodes are produced by wood-boring insects and have generally an oval or slit-like shape (BUSCHINGER et al. 1994). During colony foundation the queen might block such entrance holes with her extremely elongated head permanently or temporarily and protect the nest against intruders or water influx. The head length, (3.33–3.58 mm, $n = 20$), and head width (1.41–1.60 mm, $n = 20$) (DOROW 1996), of the queen would at least allow the blocking of smaller entrance holes (length 2.0–15 mm; width 1.0–6.0 mm; $n = 11$). Even the head dimensions of a worker ant (head length: 2.18–2.44 mm, head width: 1.25–1.41 mm, $n = 20$) (DOROW 1996) would suffice to close the smallest entrance holes. From the workers we know that at least during rain the larger entrance holes are blocked with the heads of several workers and thus protected against water influx. Thus the peculiar head shape could be a new form of head phragmosis similar to that known from other arboreal ants, e.g., *Camponotus* spp. or *Zacryptocerus* spp., which however possess truncate, round frontal head shapes and saucer shaped heads, respectively. Phragmotic structures for nest entrance or nest gallery protection are most pronounced in the queens and in the soldier caste of the concerned species (HÖLLDOBLER & WILSON 1990).

Colony size, dominance and nest hygiene

In the typical mode of the subgenus *Myrmhopla* *P. schellerichae* is arboreal, polydomous and apparently also monogynous. Its comparatively huge colony size sets *P. schellerichae* apart from the other members of the *hector*-species group, for which, as far as known, a small colony size distinctly below 1000 workers is characteristic (DOROW,

in preparation). In *P. schellerichae* we found up to ten times more workers (Table 3). This may be correlated with its special mode of life in bamboo which provides ample nesting space and a constant source of honeydew within the nest. No other non-myrmecophytic plants in South East Asia offer similar optimal nesting space for ants in such quantities. Very similar cases of a hugely enlarged colony size in comparison to their congeners are found in other bamboo specialists e.g. *P. arachne*, *P. hodgsoni* and *Tetraponera* sp. near *attenuata*. These also attain more than ten times the colony size of their congeners or species group members (DOROW & MASCHWITZ 1990, BUSCHINGER et al. 1994). We therefore can interpret the large colony size of *P. schellerichae* and that of the other quoted species as a result of their bamboo specialization.

Our behavioural studies revealed that *P. schellerichae* is a subordinate species. Despite its relatively large body size and huge colony size *P. schellerichae* avoids confrontations with other ants in its bamboo grove habitat. The endophytic way of life combined with a monopolized source of nutrition inside the nest internodes renders territorial activities other than defending the nest entrance unnecessary. Though foraging activity is reduced to a minimum, recruitment behaviour and trail laying nevertheless are developed. They are necessary traits for fast nest relocations, colony expansion to newly discovered empty bamboo internodes and contacts between the partial nests of the colony.

A further trait of the specialized endophytic life of *P. schellerichae* could be the well developed nest hygiene. The nest internodes are permanently kept free of greater amounts of decaying matter, and thus of potential sources of mould. The nests of *P. schellerichae* and *Tetraponera* sp. near *attenuata* where brood, alates and trophobionts are kept in the same place may be called stable nests in the terminology of WEISSFLOG (1991). Both species have a much smaller number of workers and detritus per stable nest (Table 3; BUSCHINGER et al. 1994) than the colonies of *Polyrbachis arachne* that were found tending *Kermicus wroughtoni* inside their nest internodes (see above) (DOROW & MASCHWITZ 1990). *Polyrbachis arachne* usually was found within a few nest internodes (2–4, $n = 10$) that contained 33–340 workers but also in a larger number of leaf pavilions (13–23, $n = 3$) that contained 3–174 workers per pavilion ($n = 22$) (DOROW & MASCHWITZ 1990).

Larval silk

All species within the *hector*-species group from which the nesting behaviour is known use larval silk for constructing and closing their nest chambers and for coating the nest walls (DOROW, in preparation). But not in a single one of the many nest internodes of *P. schellerichae* that were checked ($n = 63$) silk was used for either of these purposes. Only the brood is fixed to the nest wall with silk threads. So unlike the other members of the species group, *P. schellerichae* seems either not to use its weaving ability or even lacks it altogether. *Polyrbachis arachne*, which is also restricted to nesting in bamboo internodes usually coats the inner surface of these with a layer of silk (DOROW & MASCHWITZ 1990). This species is often found nesting in dead culm internodes, i.e. without trophobionts in the nest, while cultivating its trophobionts in silk pavilions under

bamboo leaves as a rule. But this species shows an unusual degree of flexibility. We found a) colonies without leaf pavilions tending *Kermicus wroughtoni* inside their nest internodes; b) colonies with both leaf pavilions and *K. wroughtoni* inside the nest internodes and c) colonies with trophobionts only in leaf pavilions, which is the usual case (DOROW & MASCHWITZ 1990, SCHELLERICH, LIEFKE, unpublished observations). Considering this flexible behaviour and the fact that only two colonies of *P. schellerichae* have been found so far it seems still possible that eventually colonies will be found that are using silk in nest construction. *Polyrbachis arachne* is known to narrow larger nest entrances with silk and detritus (DOROW & MASCHWITZ 1990; MASCHWITZ, unpublished observations). This species is also able to cover big holes in the nest internode (in one case nearly 1/4 of the internode wall was lacking) with a layer of silk and detritus. *P. schellerichae* was not observed to use silk in such situations. The presence of large larvae capable of silk production in most of the nest internodes speaks against a shortage of silk producing larvae being responsible for the absence of silk inside the nests. When a large part of the nest wall of one partial nest was cut away the inhabitants moved to other partial nests. *P. schellerichae* was found to use exclusively living culm internodes with trophobionts in every nest internode. The inhabitants of a nest kept in the laboratory in a petri-dish also did not use silk to reduce the size of the nest entrance (ca. 10.0 mm x 15.0 mm). These findings suggest, that nest weaving does not belong to the behaviours usually displayed by *P. schellerichae*. The fact that all other species of the *hector*-group of which the nests are known use silk for nest construction leads to the conclusion that this behaviour has been given up in *P. schellerichae*.

Nesting space is regarded as a limited resource in the rain forest (WILSON 1959) and the independence from preformed cavities through the ability to construct one's own nest should be highly advantageous in avoiding competition. It is unlikely that such an important trait is abandoned without a trade-off in other advantages. The specialization on nesting in an abundant, spacious, relatively secure and long living bamboo internode with trophobionts inside might have led to the abandonment of the weaving behaviour.

But it has to be pointed out, that the species group is no valid taxon according to the International Code of Zoological Nomenclature. Belonging to the same species group does not necessarily imply a close phylogenetic relationship. It has been created merely as an organisational tool in cases where further conclusions are not yet possible. The species groups in *Polyrbachis* are founded on few characters (alitrunk without margination, scapes and tibiae flattened in the case of the *hector*-species group) of which in most cases the functional benefits as well as the evolutionary pathways are unknown. Therefore it seems also possible, that *P. schellerichae* evolved from non-weaving ancestors and gained the morphological features of the other group members by convergent evolution in the arboreal environment.

Trophobiosis

P. schellerichae shows a highly developed trophobiotic behaviour, which definitely separates it from its species

group relatives. Generally, trophobiosis is a rare phenomenon in the genus *Polyrbachis*. *P. schellerichae* even tends its plant lice partners inside the nest internodes and manipulates them, i.e., carries them to new nest internodes during colony enlargement or nest moves. Such manipulative behaviour is known only from very few *Polyrbachis* species, among these the two other bamboo specialists *P. arachne* and *P. hodgsoni*, which mostly cultivate their trophobionts, several species of pseudococcids and aphids, in leaf pavilions (*P. arachne*) or leaf nests (*P. hodgsoni*) (DOROW & MASCHWITZ 1990). Both species collect honeydew-producing homopterans they encounter on their bamboo and carry them into their pavilions. No homopterans were present outside the pavilions unless they were strongly protected by other ants like *Crematogaster* or *Myrmecaria* (DOROW & MASCHWITZ 1990). Only three other *Polyrbachis* species, which also attain large colony sizes, *P. (Cyrtomyrma) laevissima* SMITH 1858 (DATTA et al. 1983), *P. (Myrmhopla) dives* SMITH 1857 (WASMANN 1905) and *P. (Myrmhopla) lacteipennis* SMITH 1858 (OFER 1970) are known to cultivate homopterans and display a comparable behaviour.

According to our observations the honeydew of the mealybugs inside the internodes is the main source of nutrition for *P. schellerichae*. In addition small amounts of dead prey and faeces (as nitrogen sources) are gathered. This is apparently the reason why *P. schellerichae*, though living in huge colonies, shows only minimal outside activity (Fig. 2). In consequence this species does not protect its bamboo host from herbivores, neither through patrolling activities on the bamboo nor through the active removal of herbivores, thus being more likely a mildly parasitic than a mutualistic partner. The bamboo specialist *Tetraponera* sp. near *attenuata* shows a similar behaviour (BUSCHINGER et al. 1994).

The mealybug *Kermicus wroughtoni*, which was cultivated by *P. schellerichae* in both observed colonies, however, is not a specific partner of this ant. It has been found also with other internode nesting ant species like *Tetraponera* sp. near *attenuata* (KLEIN et al. 1992), a large *Cataulacus* sp., *Crematogaster* sp. and *Polyrbachis arachne* (SCHELLERICH, MASCHWITZ, unpublished observations). An even stronger trophobiotic dependence in a bamboo specialized ant is known from *Tetraponera* sp. near *attenuata*. Its swarming queens carry mealybugs with them for colony foundation (KLEIN et al. 1992). This behaviour secures the trophobiotic nutrition of the young colony from its very beginning. Only several species of the genus *Acropyga* (Formicinae) are also known to show this behaviour (HÖLDOBLER & WILSON 1990). Our only observation of a searching winged *P. schellerichae* female on a bamboo culm (21.11.1993, shortly after 17.05 h local time) in the Gombak research area, which obviously did not carry mealybugs, makes it doubtful that a similar behaviour has developed in *P. schellerichae*.

As *Kermicus wroughtoni* is widespread on bamboo (it was found in four of five investigated bamboo groves) it possibly can invade this host plant independently. We know of such behaviour from mealybugs associated with ants of the genus *Cladomyrma* (MASCHWITZ et al. 1991). Up to now no strictly myrmecophytic ant which cultivates trophobionts is known to carry its homopteran partners with it during the nuptial flight (FIALA & MASCHWITZ 1990, MASCHWITZ et al. 1991).

Niche formation in bamboo specialized ants

Until now we have discovered three bamboo specialized ant species. *P. schellerichae* apparently is a further species that specialized in this mode of living. It is not uncommon to find two of the bamboo specialists together on the same culm or in the same grove. So do they show any form of niche differentiation? Very clear is the niche separation in *P. hodgsoni*. This species weaves together longitudinal rolled bamboo leaves and uses these for the cultivation of a variety of trophobionts and also for nesting. *P. arachne* shows a very variable behaviour as described above. Usually it builds silk pavilions beneath leaves for the cultivation of its various trophobiotic partners. The nests are often found in dead internodes which can have large irregular openings which *P. arachne* is able to close with larval silk and detritus. While *P. arachne* and *P. hodgsoni*, judged from their similar morphology and life history patterns seem to be closely related, *P. schellerichae* belongs to a different species group. It shows strong niche resemblance to the pseudomyrmecine *Tetraponera* sp. near *attenuata*. This species is polydomous and monogynous and lives in large colonies within living culm internodes. It shows an even closer trophobiosis with *Kermicus wroughtoni* than *P. schellerichae* (KLEIN et al. 1992). Both species, although having large colony sizes, do not provide any protection to their host plants and have developed an almost claustral life-style with only minimal foraging activity (KLEIN et al. 1993, BUSCHINGER et al. 1994) (Fig. 2). Slight niche differences exist concerning the size of the nest entrance. As in *P. schellerichae* the queens of *Tetraponera* sp. have elongated heads (2.36 mm x 1.26 mm, $n = 4$, $SD = 0.153$ mm and 0.077 mm). The heads of the workers are also longer than broad but not elongated (1.76 mm x 1.22 mm, $n = 4$, $SD = 0.131$ mm and 0.05 mm). While *Tetraponera* sp. only uses internodes with small entrance holes, not larger than 2.2–5.0 mm x 1.5–1.8 mm ($n = 23$) (BUSCHINGER et al. 1994), *P. schellerichae* was observed to use also internodes with larger entrances, 2.0–15 mm x 1.0–6.0 mm ($n = 11$) which are protected against intruders and water influx through entrance blocking with the elongated heads of the workers. In contrast to *P. arachne*, internodes with large openings are not accepted as nests. *Tetraponera* sp. has developed a unique defense against nest flooding. The workers drink intruding rain water and spit it out of the nest entrance, thus drying the nest interior (KLEIN et al. 1993). *Tetraponera* sp. near *attenuata* is the only known species where workers are able to bite holes into the internodes of young bamboo shoots (KOVAC 1994).

Nevertheless, apart from these special behavioural adaptations in *P. schellerichae* and *Tetraponera* sp. a wide niche overlap can be observed. So far we have not found these two species together in the same bamboo grove. As described above, 26% and 32% of the accessible culm internodes in the bamboo groves occupied by *P. schellerichae* were found to be completely empty (Table 1). The competition for nesting and living space therefore does not seem to be too extreme. TILMANN (1994), for example, developed a mathematical model (based on works of LEVINS 1969, HASTINGS 1980 and NEE & MAY 1992) which shows that it is impossible that individuals of any number of species occupy all sites in a habitat, as every species is subject to a certain rate of mortality and has a finite colonization rate. He calls his model, which he developed for plant com-

munities, the spatial competition hypothesis of diversity. In this model an inferior competitor can successfully invade a habitat, settle in a free portion of this habitat and coexist with superior competitors when either its mortality rate is sufficiently lower or its colonization rate is sufficiently higher than that of its competitors. However, this is a theoretical model that extremely simplifies the complexity of nature and, although very convincing, remains to be tested in the field. On the other hand, ROOM (1971), MAJER (1972) and LESTON (1973) introduced the concept of the ant-mosaic. This mosaic is a three-dimensional patchwork formed by non-overlapping territories of dominant ants. It has been found in the canopy of plantations and forests throughout Central and South America, Africa, Asia and northern Australia (MAJER 1993). In competition for nest-sites, foraging area and trophobionts each dominant ant excludes other dominant ants from its territory. According to ROOM (1971, 1975), TAYLOR (1977) and MAJER (1993) dominants have distinct sub-communities of non-dominant ants that are associated with them.

At the present state of our evaluation we can confirm the mosaic-like distribution of ant species in bamboo groves. When present *P. schellerichae* was a non-dominant ant. On the other hand we observed a distinct number of colony foundations of non-dominant ant species in each grove (6–22, $n = 5$). The bamboo ant community thus shows colony expansion and invasion of new species. Most probably both direct interference competition factors and indirectly working population-dynamic factors influence the bamboo ant communities which are however not static but constantly changing.

Summarized, bamboo is an extremely favourable source of nesting space and nutrition for ants and other insects, as it is not only abundant but also a stable, clumped and fast growing resource. It harbours plant-sucking insects which are apt to form trophobiotic relationships with ants. This might be the reason why during our investigation of bamboo-dwelling ant species we encountered new kinds of specializations like the one sided host-plant-specialization and the specific behavioural adaptations described here for *Polyrhachis schellerichae*.

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